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Identifying Foraging Behaviour of Wild Bottlenose Dolphins (*Tursiops truncatus*) and Harbour Porpoises (*Phocoena phocoena*) with Static Acoustic Dataloggers

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Abstract

Sound is the main means of communication for cetaceans, and studying their vocal behaviour can reveal important information about their activity patterns. As static acoustic monitoring (SAM) of whales, dolphins, and porpoises becomes more widespread, it is important to understand how data collected with automated click loggers relate to their behaviour. To assess whether behaviour can be inferred from automated click train data, echolocation click trains (series of clicks) of bottlenose dolphins and harbour porpoises recorded by C-PODs were examined with simultaneous visual observations. Recorded click trains from both species had different characteristics for the two observed behavioural categories: (1) travelling and (2) foraging. Foraging click trains for both species were of shorter duration and had shorter inter-click intervals. The distinction in the click trains between the two behaviours was stronger for harbour porpoises. More than one quarter of the harbour porpoise click trains represented a distinct group of very fast click trains or "buzzes," which were thought to be associated with foraging, whereas only a small fraction of such trains was found in the bottlenose dolphin click data. For both species, the C-PODs showed potential in detecting foraging behaviour and in identifying potential feeding sites and trends in foraging activity.

Key Words: bottlenose dolphin, *Tursiops truncatus*, harbour porpoise, *Phocoena phocoena*, foraging, feeding, C-PODs, inter-click interval, echolocation, vocal behaviour

Introduction

The protection of a threatened species requires conservation and management of its habitat and the ecosystem upon which it relies. For large, mobile marine mammal species, it is not practical to designate their entire habitats as protected areas; therefore, it is essential to identify those areas which, if protected, would be most beneficial to the species' survival such as those used for feeding or breeding (Hoyt, 2004). To assess impacts of threats on populations, it is important to investigate trends in foraging or breeding success, in addition to monitoring animal abundance (Fiedler & Jain, 1992). For marine mammals, this typically requires visual observations of behaviour, which can be expensive and often require a lot of manpower, especially when it requires techniques that include aerial or boat-based surveys, photo-identification, or tagging (Evans & Hammond, 2004). Many studies of cetaceans rely purely on behavioural observations during surfacing, but details of behaviour can be difficult to identify accurately with visual observations conducted from above the water's surface. Cetaceans are only visible at the surface for between 1 to 10% of the time (Tyack & Miller, 2002), making classification of animal activity based on their vocalizations more appropriate (Martin & Reeves, 2002). Cetaceans echolocate more frequently than they produce other types of sounds, possibly due to the energetic costs of whistles in comparison to clicks (Jensen et al., 2012). One method of monitoring echolocation activity is to deploy static acoustic data loggers, such as C-PODs, to record click trains (Dudzinski et al., 2011).

The two study species, the bottlenose dolphin (*Tursiops truncatus*) and the harbour porpoise (*Phocoena phocoena*), produce very different vocalizations. The bottlenose dolphin emits sounds in three broad structural categories: (1) burst-pulse sounds, (2) whistles, and (3) clicks (Caldwell et al., 1990; Tyack, 1997). It is thought to use echolocation clicks mainly for navigation and foraging, while burst-pulse sounds and whistles are used for communication (Mann et al., 2000; Janik, 2009), although it is highly likely that clicks also serve a communicative function (Tyack, 1997). By contrast, the harbour porpoise only produces clicks and is thought to use these for navigation, foraging, and communication (Verboom & Kastelein, 2003; Koschinski et al., 2008; Verfuß et al., 2009; Clausen et al., 2010). This study focuses on the characteristics of echolocation click trains recorded from both species during different behaviours.

Harbour porpoise clicks have been shown to have mean source levels ranging from 157 to 191 dB re 1 μPa (peak-to-peak) @ 1 m, click durations dependent on the click repetition rate between approximately 77 to 300 μs, and a peak frequency around 125 to 131 kHz (Au et al., 1999; Teilmann et al., 2002; Villadsgaard et al., 2007). Bottlenose dolphin clicks are shorter and more varied, with measured source levels of 177 to 228 dB re 1 μPa (peak-to-peak) @ 1 m, click durations of 8 to 72 μs, and peak frequencies between 30 to 150 kHz (Au et al., 1974; Au & Hastings, 2008; Wahlberg et al., 2011). Inter-click intervals (ICIs) vary with context for both species. Bottlenose dolphins steadily decrease their ICIs with decreasing distance to a target (Jensen et al., 2009). For harbour porpoises, ICIs of around 50 to 60 ms have been reported from small data samples during their initial navigation/search phase (Au, 1993; Akamatsu et al., 2005; Villadsgaard et al., 2007). They are thought to switch to a decreasing ICI only when "range locking" upon a target, and finally end with a terminal buzz with an ICI of around 1.5 ms (during maximum click repetition rate) when reaching the target (Verboom & Kastelein, 2003; Villadsgaard et al., 2007; Verfuß et al., 2009). Both bottlenose dolphins and harbour porpoises are able to adjust the properties of their echolocation signals to allow for varying target range and multiple target selection (Jensen et al., 2009; Wisniewska et al., 2012). Both species project their echolocation clicks in a directional beam, with most of the acoustic energy directly in front of the animal, approximately 9 to 10° wide for bottlenose dolphins (Au et al., 2012) and 13° for harbour porpoises (Koblitz et al., 2012). Bottlenose dolphins produce intense, short broadband clicks, whereas harbour porpoises produce only narrowband clicks centred around 130 kHz (Au, 1993; Wahlberg et al., 2011; Koblitz et al., 2012). As higher frequencies are more rapidly absorbed by sea water, the higher intensity and lower frequency bottlenose dolphin clicks travel further than those of harbour porpoises.

Most of the literature describing bottlenose dolphin or harbour porpoise echolocation focuses only on clicks recorded near the relative beam axis—the so-called "on-axis" clicks. However, the farther away from the beam axis the clicks are recorded, the more altered they become. The "off-axis" clicks from dolphins have lower frequency and amplitude characteristics to the on-axis clicks (Au & Hastings, 2008), which results in a high number of clicks with dominant frequency in the lower part of the frequency range, making the dolphin clicks recorded by C-PODs more variable. The quieter, more narrowband, high-frequency clicks of the harbour porpoise show very little off-axis click frequency variability and, thus, are easier to recognize and classify, particularly when using automated algorithms such as those utilised by the C-POD's software. Despite the distinct characteristics of clicks, there are occasions in which individual bottlenose dolphin clicks can seem very similar to harbour porpoise clicks, and this can cause errors in species classification when using automated click detection systems (Simon et al., 2010).

Both species alter their vocalizations according to function and behaviour. Bottlenose dolphins emit different types of vocalizations used for different behaviours (Nowacek, 1999, 2005; Acevedo-Gutiérrez & Stienessen, 2004; Quick & Janik, 2008; Janik, 2009; Simard et al., 2011). For harbour porpoises, which produce only one type of vocalization (the high-frequency click), differences in click train characteristics, particularly the ICI, relate to behavioural context (Akamatsu et al., 1994; Verfuß et al., 2009; Clausen et al., 2010).

Although echolocation in bottlenose dolphins and harbour porpoises is relatively well studied, few attempts have been made to investigate the influence of behaviour on click train characteristics. Those studies that have examined vocal behaviour in this context have been largely conducted in captivity, and information on wild vocal behaviour involving signal characteristics is generally lacking (Au, 1993).

Previous studies have reported varying harbour porpoise ICIs, with progressively falling ICIs during foraging ending in a high rate "buzz" of 300 to 600 clicks/s (Verboom & Kastelein, 2003; DeRuiter et al., 2009; Miller, 2010; Wisniewska et al., 2012) with an extremely short ICI of max. 1.5 ms (Verboom & Kastelein, 2003; Verfuß et al., 2009) during the final prey capture. For bottlenose dolphins, studies have shown that echolocation rates (the number of clicks recorded in a time unit) vary according to different behaviours (Jones & Sayigh, 2002), and that during foraging, bottlenose dolphins produce shorter and faster clicks (termed *feeding buzzes*) with the shortest ICIs reported between 3.0 and 7.1 ms (Wahlberg et al., 2011).

C-PODs and their predecessors, T-PODs, are acoustic data loggers developed to record information about odontocete echolocation clicks and are widely used to monitor cetacean presence (Carstensen et al., 2006; Rayment et al., 2009; Simon et al., 2010). Some studies have also used

T-POD data to identify harbour porpoise foraging behaviour (Koschinski et al., 2008), and to characterize click train characteristics of foraging and travelling dolphins (Reyes Zamudio, 2005; Bond, 2006). The use of static click loggers as an alternative to broadband hydrophones with recording gear has its advantages as they are relatively inexpensive, easy to use with small data storage requirements, have automated click train detection, and can be left *in situ* for several months. The C-POD detects pulsed sounds in the 20 to 160 kHz range and records the time and duration to 5 µs resolution, the dominant frequency, and a range of click characteristics. This selective logging limits the amount of data stored. Continuous broadband recording with 16-bit resolution at 500 kHz sampling rate generates about one terabyte of data every 10 d, whereas the C-POD's four gigabyte memory card can last up to 5 mo. This study explores the use of C-POD click train data to identify different behavioural states for both bottlenose dolphins and harbour porpoises by comparing click train characteristics and visually observed animal behaviours. Additionally, the occurrence of potential feeding buzzes based on ICI criteria is examined for both behavioural categories.

Methods

Data Collection

The study was conducted within the Cardigan Bay Special Area of Conservation (SAC), West Wales, from February to July 2010. A total of 33 manufacturer-calibrated C-PODs were deployed in a grid formation in front of the observation site for 151 d at water depths of 17 to 22 m, with each C-POD approximately 1 m above the seabed. During this period, visual observations of the area around the C-PODs were conducted on 72 d for a total of 261 h from a cliff-top monitoring site on the New Quay Headland within the SAC (Latitude: 52° 13.040 N, Longitude: 04° 21.871 W ± 5 m).

Calibration of C-PODs

The sensitivity of the C-PODs had been tested after manufacturing by rotating each unit in a sound field. The sensitivity of the unit had then been adjusted to achieve a radially averaged, temperature corrected, max source pressure level reading within 5% of the standard at 130 kHz (± 0.5 dB). These radial values were taken at 5° intervals. After the experiment, the units were sent to the manufacturer for recalibration which showed that all units were within the original specifications after 2 y of use and that there were no changes of operational significance. This calibration and standardization procedure is accessible in detail on the manufacturer's website (www.chelonia.co.uk).

Visual Observations

Visual observations were conducted by two to four observer teams in sea states ≤ 3 over a visible sea-surface area of approximately 3-km radius around the deployed C-PODs from a cliff top at 93 m from the sea surface. Although the *effective* detection area where bottlenose dolphins and harbour porpoises are detected with C-PODs is relatively small, around 300 to 400 m for bottlenose dolphins and approximately 150 to 200 m for harbour porpoises, depending on behaviour, all observed data were included in the analysis since maximum detection distances with C-PODs span beyond the effective area (Nuuttila, 2012). During animal sightings, observers recorded behaviour, group size, travel direction, group composition, and group cohesion. Binoculars with magnification of 8 × 32 and a 30× magnification Sokkia electronic digital theodolite (DT5A) were used to aid detection and tracking of the study animals. A group of animals was described as "a number of dolphins or porpoises in close association with one another, often engaged in the same activity and remaining within approximately 100 m of one another" (Shane, 1990; Bearzi et al., 1999). To ensure that the acoustic and visual data originated from the same group of animals, all periods with multiple groups were excluded from the analysis.

Behaviour was defined using the following categories: foraging/feeding (visible surface foraging and prey pursuit/capture where fish seen fleeing, tossed about, or in the bottlenose dolphin's mouth; feeding birds circling above the dolphins; fish shoals visible under the surface; and demersal foraging consisting of repetitive, long feeding dives in the same location), socializing (physical contact, chasing each other, mating, synchronised movement, aggression, and play), aerial behaviour, travelling, and milling (where dolphins are moving in varying directions with no observable surface behaviour) (Shane, 1990; Bearzi et al., 1999). Because of the low number of observations in some of the behaviour categories (e.g., only 24 min of resting behaviour reported for bottlenose dolphins), only the foraging/feeding and travelling categories were used for analysis. Typically, the term *foraging* describes the search for food while *feeding* is the actual event of food intake. Herein, the category *foraging/feeding* comprised both foraging and feeding activities, which for echolocating cetaceans typically involves producing high-frequency echolocation clicks. *Feeding buzzes* were defined as those clicks with ICIs of less than 10 ms duration that are produced during feeding (Verfuß et al., 2009). Environmental data with sea state, swell height, cloud cover, visibility, and tidal height were collected at 15-min intervals to assess the observation conditions so that sightings made during poor sighting conditions (e.g., rain, fog, or sea state > 3 in the Beaufort scale) would not be used for further analysis.

Acoustic Data

The data were downloaded using *CPOD.exe*, and the click trains (series of clicks) in the acoustic data were identified with the KERNO classifier that is part of the post-processing software. Click trains logged on a static logger are generally only brief fragments of longer click trains made by the animal and captured as the animal's sound beam sweeps across the hydrophone. Click train duration therefore represents the speed of such sweeping movements and is not a measure of the full duration of click trains produced. Click trains are automatically classified by the KERNO classifier into four quality classes according to their likelihood of being correctly classified as originating from cetaceans. Click trains classified into the three highest quality classes—high, moderate, and low—were used in the study, while *doubtful* click trains were disregarded. After consulting the manufacturer, low-quality click trains were included in the analysis since the study area has low levels of background noise, and low-quality click trains showed a strong temporal association with high- and moderate-quality click trains. The algorithm also assigns each click train to a species class: *porpoise* (also called narrowband high frequency [NBHF]), *dolphin*, or *boat sonar*. To avoid potential false classification by the algorithm, only data recorded during visual observations of single species were used. Additionally, a visual validation of click train identification was performed using the graphical data presentation in *CPOD.exe* on 100 systematically selected click trains of both species. This resulted in one potential false positive harbour porpoise detection and two potential false positives in the bottlenose dolphin data. For bottlenose dolphins, both false positives were thought to originate from a harbour porpoise. To avoid problems with erroneous species classification, only single species sightings were included in the analysis. Visual and acoustic data were matched by time, and each minute of acoustic data was assigned a behavioural category from the simultaneous visual observations.

A total of 13 different click train characteristics recorded by the C-POD were investigated for both bottlenose dolphin and harbour porpoise data (Table 1). Click trains with ICIs of unusually long duration (possibly resulting from solitary clicks which the algorithm grouped together as single click trains) were removed.

First, the click train characteristics for both species were described for the entire acoustic data. This was then repeated for those minutes that had matching visual observations. The acoustic dataset was then inspected for underlying structure between the characteristics using multidimensional scaling (MDS). Patterns in the distribution of ICIs were used to identify distinct groups of click trains with similar minimum and average ICIs. Click trains were considered as outliers and removed if they had ICIs longer than 450 ms for bottlenose dolphins and 250 ms for harbour porpoises.

Comparison of Click Trains Between Different Behaviours

Click trains recorded during observed foraging/feeding and travelling behaviour were compared to examine for potential differences in click train characteristics using Wilcoxon rank sum *W* tests (Mann-Whitney-Wilcoxon). A generalized linear model (GLM) with binomial errors, MDS, and an analysis of similarity (ANOSIM) were also used to investigate similarity within predefined groups of click characteristics for the two behaviour categories.

Identifying Feeding Buzzes Based on ICI Criteria

Following previous studies, fast click trains with a minimum ICI of < 10 ms were used as a proxy for potential feeding activity (Carlström, 2005; Verfuß et al., 2009). The ratio of these *feeding buzzes* to *non-feeding buzzes* and the total echolocation rate recorded were then calculated for the two different behavioural categories (Todd et al., 2009). Both total number of clicks/min and the number of click trains/min were calculated in order to assess the total amount of vocalisation produced (and recorded) by the C-POD.

Table 1. Echolocation click train characteristics recorded by C-PODs used to compare click trains. ICI = inter-click interval; SPL = sound pressure level.

Characteristic extracted from C-POD data	
Click train duration (μs)	Modal frequency (kHz)
No. of clicks/train	Mean end frequency (kHz)
Clicks/s	Minimum frequency (kHz)
Maximum ICI (μs)	Maximum frequency (kHz)
Minimum ICI (μs)	Maximum SPL*
Mean ICI (μs)	Mean SPL*
Last ICI in a click train unit	

*Received SPLs recorded by C-PODs are on a linear scale that varies with frequency and are the peak-to-peak SPLs of the loudest cycles within the clicks. The data logged on each click are insufficient to calculate a true intensity for the click. The SPL scale's upper limit is often exceeded by loud clicks, which are then logged as having the highest SPL scale value

Results

During the 151 d of deployment, C-PODs recorded 42,716 min of bottlenose dolphin detections and 75,015 min of harbour porpoise detections. There were 88 visual sightings of bottlenose dolphins and 26 of harbour porpoises in the observed area. Of the total visual observation time, 139 min were considered suitable for further analysis. A total of 1,106 click trains matched the selected visual observation times, of which 570 were bottlenose dolphins and 536 were harbour porpoises.

Entire Acoustic Dataset

Both bottlenose dolphin and harbour porpoise click train characteristics matched those reported in the literature for frequency range and for average and minimum ICI (Table 2). The distribution of ICIs of click trains classified as stemming from harbour porpoises had a distinct peak of very short ICIs of less than 2.5 ms, whereas bottlenose dolphin click trains had three peaks, at less than 2.5 ms, at around 65 ms, and at around 135 ms (Figure 1). The average centre frequency of individual harbour porpoise clicks within a click train was concentrated around 130 kHz, whereas the average centre frequency of bottlenose dolphin click trains varied between 25 and 120 kHz. The C-POD records a relative amplitude parameter for the received SPLs of each click (confusingly termed SPLs, but care must be taken not to confuse this with the widely used acronym for *source pressure level*). This parameter is shown on a linear scale which varies with frequency and is the peak-to-peak SPL of the loudest cycles within the clicks. The data logged on each click are insufficient to calculate a true intensity for the click. The SPL scale's upper limit is often exceeded by loud clicks, which are then logged as having the highest SPL scale value. Herein, the harbour porpoise clicks showed little SPL variation and relatively low values of < 50 SPL units, whereas the SPL values for bottlenose dolphin clicks ranged from 10 to 160 units, indicating large differences in the SPLs (Figure 2).

There was a positive correlation between click train duration and minimum ICI for both species, shorter click trains having the shortest ICIs, notably during visually observed foraging/feeding events (HP: $r = 0.75$, $t = 26.24$, df = 534, $p < 0.001$; BND: $r = 0.5521$, $t = 15.78$, df = 568, $p < 0.001$).

Differences Between Foraging/Feeding and Travelling Click Trains

Harbour porpoise foraging/feeding click trains were shorter in duration, had faster repetition rates, and lower ICIs than travelling click trains. Harbour porpoise click trains also had lower frequencies recorded in all frequency categories and lower received maximum SPLs compared to travelling click trains. Similarly, bottlenose dolphin foraging click trains were shorter and faster than travelling click trains, but the differences between click trains recorded in foraging/feeding vs travelling contexts were not as obvious as for harbour porpoises (Figure 3). According to Wilcoxon rank sum *W* tests, 10 characteristics were significantly different between the two behaviour categories

Table 2. Summary of harbour porpoise (HP) and bottlenose dolphin (BND) echolocation click train characteristics detected by C-PODs during the whole of the acoustic deployment period; mean values (± SD) are shown. ICI = inter-click interval; SPL* = sound pressure level.

Click characteristic	HP median	HP mean	HP SD	BND median	BND mean	BND SD
Click train duration (ms)	207.99	371.08	482	1,029	1,259	1,012
No. of clicks/train	7	10.1	7.4	8	10.7	6.4
Clicks/s	37	102	151	7	20	51.2
Maximum ICI (ms)	33.1	55.9	62.3	169	177	1,132
Minimum ICI (ms)	25.3	44.0	49.3	126	134	85
Mean ICI (ms)	27.1	46.2	56.8	138	142	87
Last ICI in a click train	30.0	52.4	60	156	169	1,155
Modal frequency (kHz)	129	130	5.5	47	50	19.9
Mean end frequency (kHz)	126	126.2	5.7	61	63	21.8
Minimum frequency (kHz)	125	124.4	7.6	37	39	14.0
Maximum frequency (kHz)	134	134.7	5.4	101	95	33.6
Maximum SPL*	40	68.9	66.1	173	159	80.7
Mean SPL*	28.0	39.9	33.2	68	73	43.1
n	1,376,594			272,317		

* Unreferenced SPL derived from *CPOD.exe* software output; see Table 1.

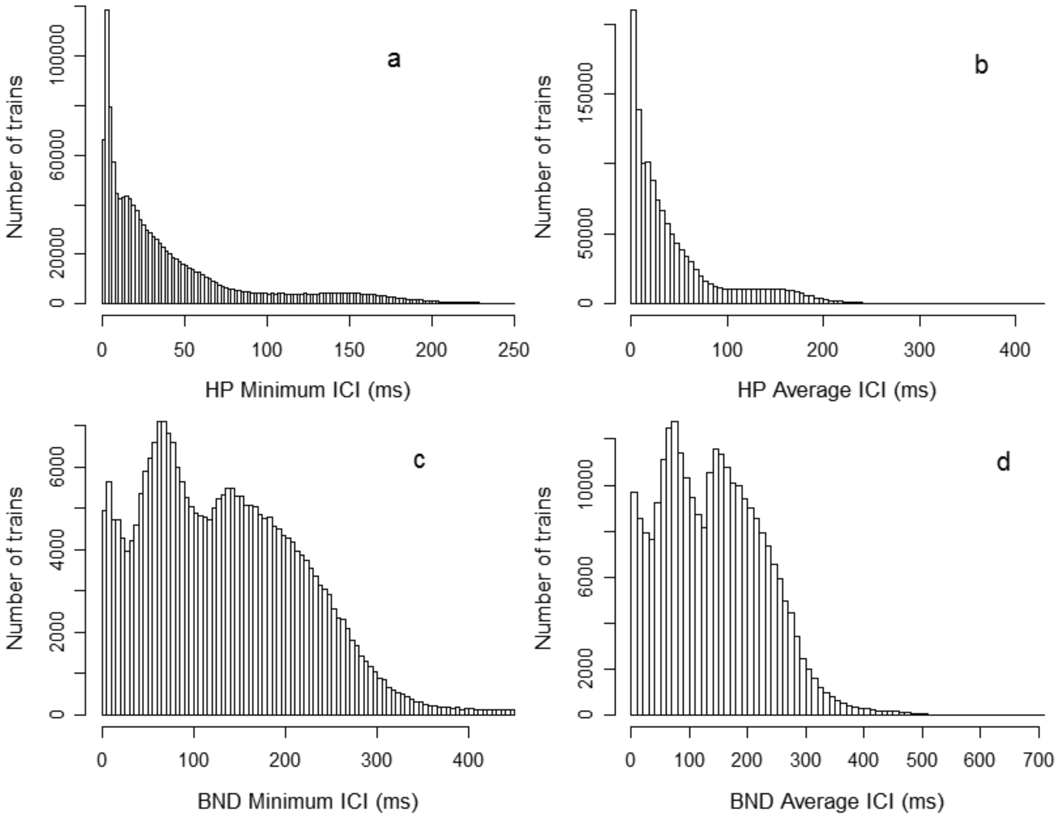

Figure 1. Histograms of minimum and average inter-click intervals (ICI) for harbour porpoise (HP) (a and b) and bottlenose dolphin (BND) (c and d) click trains

for harbour porpoise, while six were different for bottlenose dolphin (Table 3).

Analysis of Similarity and Multidimensional Scaling
ANOSIM within harbour porpoise click characteristics revealed significant differences of click trains between those recorded during observed foraging/feeding and travelling sightings (R = 0.2333, $p < 0.001$, 999 permutations). No significant difference was found in bottlenose dolphin click trains for foraging/feeding and travelling animals (R = -0.08403, $p = 1$, 999 permutations). Similarly, no difference in bottlenose dolphin click trains was found from the MDS (Figure 4).

Generalized Linear Model
The GLM with binomial errors conflicted with the ANOSIM analysis as it indicated that behaviour contributed significantly to explaining the observed differences in click characteristics for *both* study species. For harbour porpoises, modal frequency and (log transformed) clicks/s were the two variables that best explained the difference between foraging/feeding and travelling animals (according to AIC model selection). For bottlenose dolphin data, the selected variables were minimum ICI, average (relative) SPL, clicks/s, and maximum frequency. Although clicks/s was not a significant variable, it was nevertheless selected for the best model according to AIC values.

Identifying Foraging/Feeding Click Trains Based on ICI Criteria
For both species, there was a peak of click trains with very short ICIs, indicating possible foraging behaviour (Figure 1). This was particularly notable in the harbour porpoise data, with 27.3% of click trains classified as potential feeding buzzes with minimum ICIs of < 10 ms. Only 3.8% of the bottlenose dolphin click trains had minimum ICIs under 10 ms. Furthermore, 16.8% of all harbour porpoise click trains had a minimum ICI of less than 5 ms, whereas only 1.8% of bottlenose dolphin data had such short ICIs.

The ratio of these feeding buzzes to non-feeding buzzes in harbour porpoise data was higher for

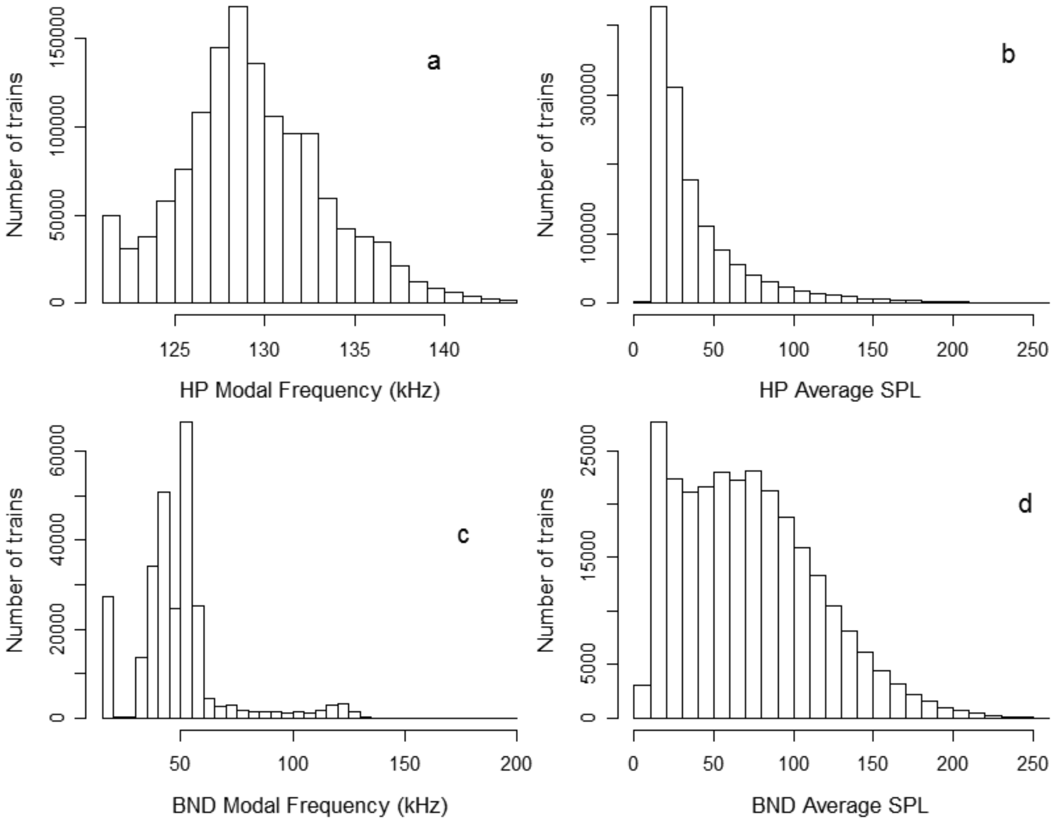

Figure 2. Histograms of modal frequency and average received relative SPLs* for harbour porpoise (HP) (a and b) and bottlenose dolphin (BND) (c and d) click trains

* Unreferenced SPL derived from *C-POD.exe* software output; see Table 1.

Table 3. Summary of Wilcoxon rank sum *W* tests (Mann-Whitney-Wilcox) comparing median click train characteristics detected by C-PODs which corresponded to visually observed bottlenose dolphin (BND) and harbour porpoise (HP) groups engaged in feeding and travelling. ICI = inter-click interval; SPL* = sound pressure level. Number of click trains analysed: BND – feeding/foraging, *n* = 424; travelling, *n* = 146; HP – feeding/foraging, *n* = 163; travelling, *n* = 373. Marked in bold are those characteristics that were most influential variables in binomial GLM.

Click characteristics	HP *W* test statistic	HP *p* value	BND *W* test statistic	BND *p* value
Click train duration (µs)	11,102	< 0.001	20,121	< 0.001
No. of clicks/train	20,695	0.9718	26,199	0.569
Clicks/s (log transformed)	**45,605.5**	**1**	**37,277.5**	**0.999**
Maximum ICI (µs)	10,198	< 0.001	**19,924**	**< 0.001**
Minimum ICI (µs)	9,913.5	< 0.001	20,386	< 0.001
Mean ICI (µs)	10,143.5	< 0.001	20,537	< 0.001
Last ICI in a click train	10,186.5	< 0.001	20,942	< 0.001
Modal frequency (kHz)	**11,768**	**< 0.001**	27,591	0.863
Mean end frequency (kHz)	11,799	< 0.001	22,482	0.011
Minimum frequency (kHz)	11,526.5	< 0.001	28,470	0.953
Maximum frequency (kHz)	12,466	< 0.001	19,542	< 0.001
Maximum SPL*	15,563.5	< 0.001	**23,879**	**0.086**
Mean SPL*	16,502.5	0.03022	**27,832**	**0.895**

* Unreferenced SPL derived from *C-POD.exe* software output; see Table 1.

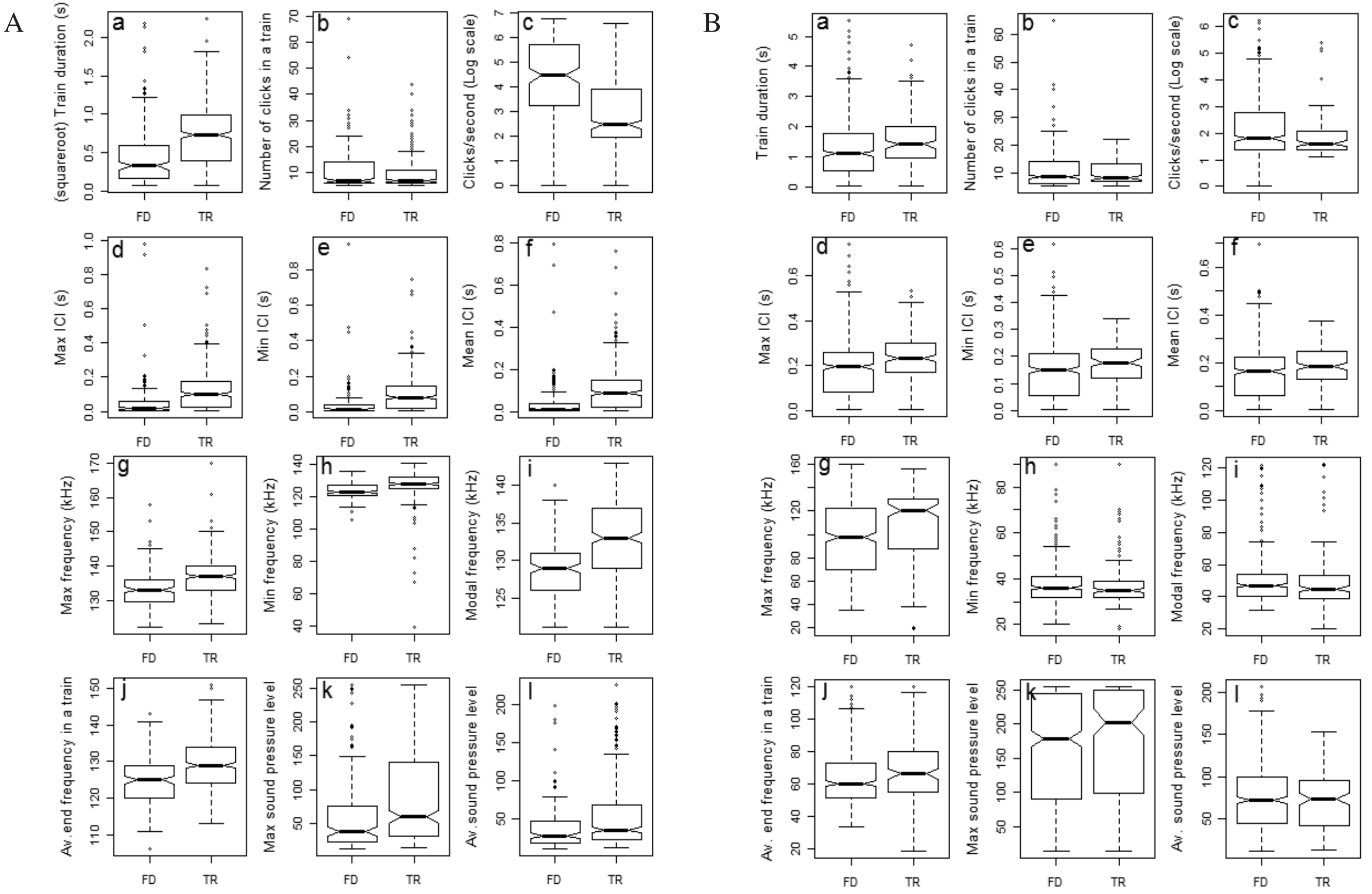

Figure 3. Box plots depicting selected (A) harbour porpoise and (B) bottlenose dolphin click train characteristics by behaviour: feeding/foraging (FD) and travelling (TR). Characteristics: (a) click train duration, (b) number of clicks in a train, (c) clicks/s, (d) maximum ICI, (e) minimum ICI, (f) mean ICI, (g) maximum frequency, (h) minimum frequency, (i) modal frequency, (j) average end frequency, (k) maximum (unreferenced) SPL, and (l) average (unreferenced) SPL. Box represents the interquartile range (IQR), with whiskers extending up to 1.5 times IQR, thick black lines are median values, circles mark outliers, and width of the box indicating sample size. If the notches in box plots do not overlap, the medians are significantly different to the 5% level ($p < 0.05$), assuming asymptotic normality around medians and roughly equal sample sizes.

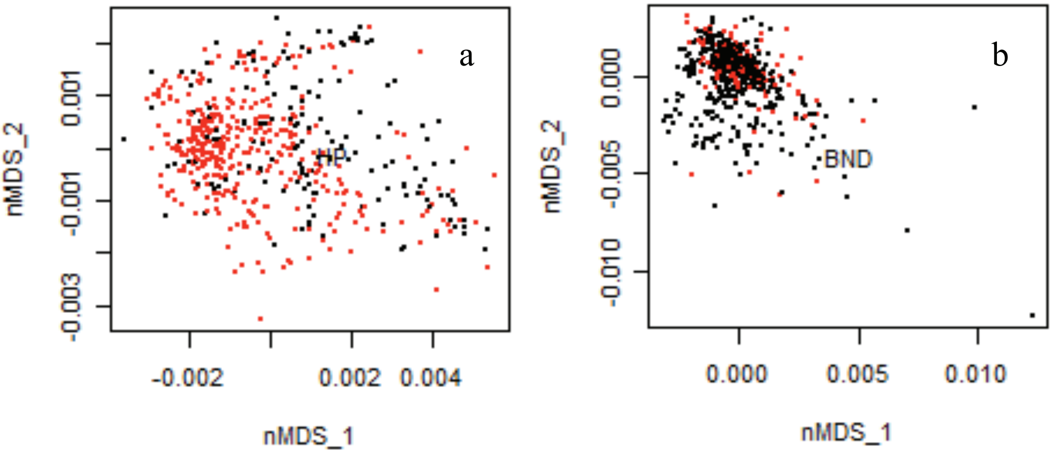

Figure 4. Multidimensional scaling (MDS) plots for harbour porpoise (a) and bottlenose dolphins (b) for log transformed click train characteristics by behaviour, feeding/foraging (black), and travelling (red)

click trains recorded during observed foraging/feeding events in comparison to click trains from travelling ones, but there was no such difference in the bottlenose dolphin data (Figure 5). The echolocation rate (for total numbers of clicks produced and number of click trains) was higher for foraging harbour porpoises but lower for foraging bottlenose dolphins in comparison to travelling animals (Figure 5).

The percentage of recorded feeding buzzes was higher during those minutes where the animals were identified as feeding/foraging, but notably so for the harbour porpoises (Figure 6).

Discussion

This study demonstrates that the C-POD click logger together with its associated software is able to identify and distinguish click trains from both bottlenose dolphins and harbour porpoises, and that the resulting click trains have similar characteristics to those described in the literature from direct measurements. The software produces several output characteristics but not all are useful for further analysis. Click train classification software does not necessarily identify all the clicks of a train with similar probability; and some may go unclassified, while other non-cetacean clicks may be included in the click trains. For example, the minimum and maximum frequency characteristics may be affected by these accidental non-cetacean clicks thus obscuring real animal clicks. For this reason, the modal frequency of a click train may be more representative of the actual frequency. In cases where there are few detections, or long periods between detections, the software may merge clicks to form trains or alternatively cut click trains short, thus causing artificially long or short click train durations and potentially erroneous average or minimum ICIs. In fact, click train duration is more descriptive of the speed of the animal's head movement than is the actual vocalization. Additionally, subsequent click trains of very similar characteristics may be of different quality class, in which case the selected quality class will affect the end results. To avoid these issues, only quality classes high, medium, and low were included, and click trains that had outlier ICI values longer than 450 ms for bottlenose dolphins and 250 ms for harbour porpoises were discarded.

Minimum ICI and click train duration were correlated for both species so that short click trains were also fast click trains, indicating that animals sweep their heads from side to side while vocalizing. Another reason which may cause very short buzzes to be missed by the C-POD is the lower amplitude levels of buzzes, causing even less of the buzz to be detectable by the C-POD and therefore only partial click trains to be recorded.

Click trains from harbour porpoises had a distinct peak, with a high number of recorded click trains containing very short ICIs. Such a peak was not present in the bottlenose dolphin data, which instead had three distinct groupings of ICIs. This could indicate that bottlenose dolphins use clicks with varied ICIs, producing clicks with short and longer ICIs, whereas harbour porpoises mainly produce clicks with very short ICIs during the last phase of foraging. This might explain why there was a clearer distinction between the two behaviours in the C-POD data from harbour porpoises.

When assessing those click trains that were recorded during periods of visual observation, it is evident that both click train duration and minimum ICI recorded during observed foraging were

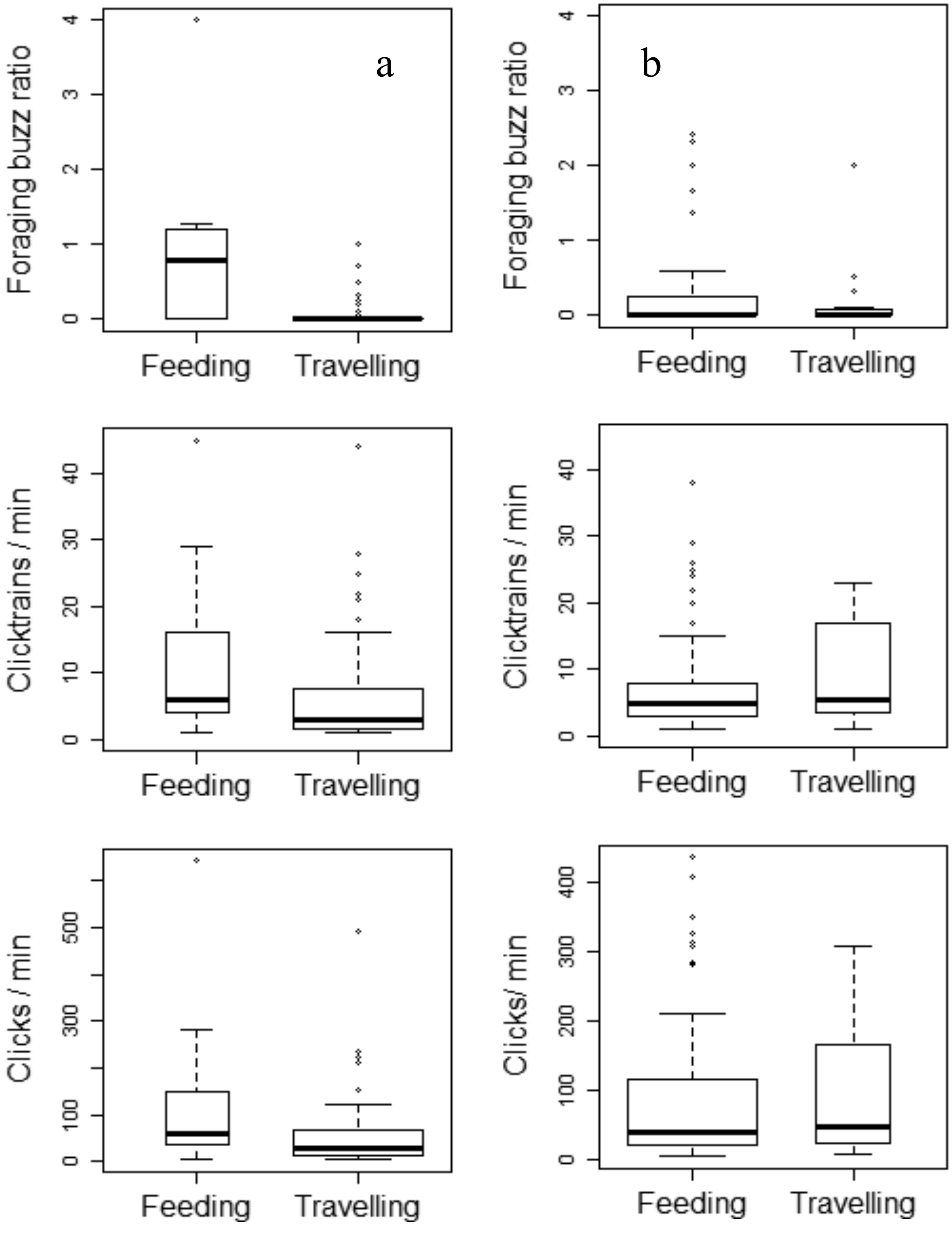

Figure 5. Ratio of feeding buzzes (click train ICIs < 10 ms) to non-feeding buzzes for harbour porpoises (a) and bottlenose dolphins (b) for both behavioural categories (top); also shown is the echolocation rate in number of click trains (middle) and number of clicks recorded per minute (bottom). See Figure 3 for explanation of box plots.

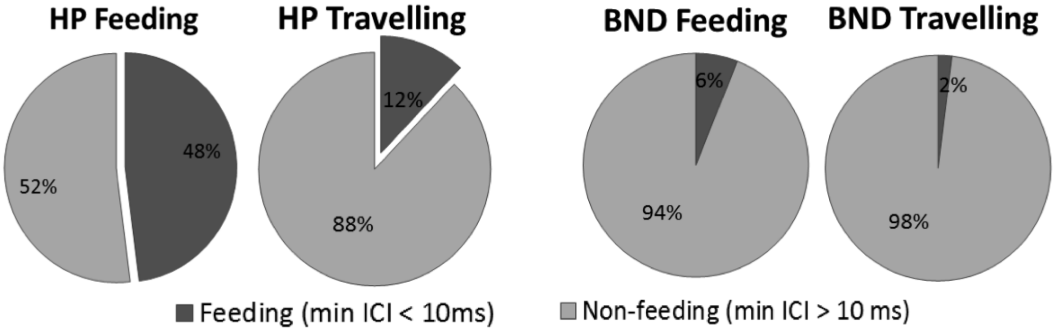

Figure 6. Percentage of feeding buzzes (with click trains of minimum ICI < 10 ms) within both behavioural categories for both species

shorter than those recorded during travelling for both species. Interestingly, for both species, the click trains are of greater intensity (relative SPL) and of higher frequency in travelling animals. This fits with previous studies where click frequency content was found to correlate with click amplitude (Beedholm, 2010). This finding is consistent with the theory that travelling animals are interested in interpreting the acoustic scene further ahead, thus requiring more intense clicks with longer ICIs to read echoes from distant targets. This is particularly interesting for harbour porpoises as they have so far not been shown to vary their click frequency according to behaviour (Clausen et al., 2010). It must be noted, however, that the SPL of bottlenose dolphin clicks often exceeds the upper limit of the sound pressure scale of the C-POD.

For harbour porpoise data, the difference between foraging and travelling click trains was statistically significant using all three methods of analysis (non-parametric Wilcoxon-Mann-Whitney, GLM, and ANOSIM), whereas the ANOSIM did not indicate statistically significant differences in click trains between the bottlenose dolphin behaviours. Furthermore, the percentage of click trains which corresponded to the "correct" visually observed behavioural classification was much higher in the harbour porpoise data than in the bottlenose dolphin data.

There are a number of potential explanations for these results: (1) the dataset was not representative of the two behaviour categories investigated here and the power of these tests was thus reduced; (2) bottlenose dolphins simply do not produce different clicks for these two behaviours; or (3) the distinction between observed foraging/feeding and travelling behaviours was erroneous. The accuracy of the visual classification of behaviour is important since the animals only spend a fraction of time on the surface, and despite careful descriptive categories, this classification is inherently subjective (Similä & Ugarte, 1993). For this research, the observations were carried out only on days with good visibility using visual aids (binoculars and theodolite), and the most experienced observer would confirm the assigned behavioural category depending on his or her judgment of animal movement and speed and any additional information such as feeding birds or visible fish shoals. In order to avoid misclassification, data from encounters for which behaviour was frequently changing between the two or where combined foraging and travelling were observed were omitted from the analysis. Additionally, data from encounters of more than one species, and of encounters with several animals engaged in differing behaviours were excluded, thus reducing the amount of potential observer bias. Furthermore, misclassifications would be expected to erode the level of significance of the acoustic discrimination, but as this has proved statistically significant, it could be seen as validating the visual classification.

Another explanation for why the data may not be entirely representative of foraging/feeding vocalizations is if some of the bottlenose dolphin foraging click trains (such as click trains with very short ICIs) were not recorded by the C-PODs or, even if recorded, they did not fit the algorithm's classification criteria. It is important to note also that C-PODs, like any static acoustic devices, are confined to their mooring location; only those clicks which are directed towards the device and which are produced at the device's detection range are detected. The effective detection radius with C-PODs has been estimated to be around 300 to 400 m for bottlenose dolphins and around 150 to 200 m for harbour porpoises, depending on animal behaviour; however, C-PODs have been found to detect clicks from over 1,500 m for bottlenose dolphins and over 500 m for harbour porpoises (Nuuttila, 2012). Herein, we used detections from animals up to 1,500 m away to maximise our sample size.

Of the click trains that were recorded during behavioural observations, over 70% were during foraging events, and yet only 3.8% were classified as feeding buzzes with a minimum ICI of less than 10 ms. The comparative absence of fast clicks in the bottlenose dolphin data could be the result of decreased source levels of the feeding buzzes which would make them undetectable to the C-POD. Alternatively, if they were too similar to harbour porpoise clicks, fast clicks from bottlenose dolphins might be discarded by the software's click train classification process.

Although bottlenose dolphins are capable of adapting their source levels to suit their surroundings (Jensen et al., 2009), emitting intense clicks in shallow water can create high levels of reverberation due to sound reflecting from both the surface and seabed (Zimmer, 2011). A single bottlenose dolphin click in shallow water is thus commonly received as a cluster of many clicks arriving along different pathways. This may result in many click trains from those animals close to the logger not being identified as click trains. C-PODs are designed to detect click trains, and as the C-POD does not log the shortest, most broadband clicks or the lower part of the vocal repertoire (< 20 kHz), and it includes off-axis clicks, the clicks recorded by C-PODs are a relatively inaccurate representation of the actual vocalizations produced. This is likely to be particularly problematic when attempting to classify or characterise dolphin clicks.

The lack of feeding buzzes (clicks with very short ICIs) in the bottlenose dolphin data would also explain why the echolocation rate for bottlenose dolphins is actually lower for foraging animals than for travelling animals, contrary to what was expected based on previous studies (Tyack, 2000; Nowacek, 2005). An alternative explanation could be that the bottlenose dolphins considered to be foraging were actually involved in more complex search behaviour (Bailey & Thompson, 2006) and were not producing feeding buzzes until within very close proximity to a fish. Perhaps feeding buzzes are more frequently used on demersal or benthic prey, which are highly camouflaged and lie still on the seabed for the majority of the time (Gibson, 2005). This could conceivably make the use of buzzes more necessary than when feeding on fish shoals in the water column. If feeding buzzes are directed towards the seabed, a large part of the sound's energy may be absorbed in the seabed and, due to the directional nature of feeding buzzes, will not be able to ensonify the C-POD's hydrophone and therefore will not be detected.

There were insufficient visual observation data to assess the click characteristics potentially related to other behavioural categories such as milling, resting, or socialising, which also form an important part of these species' behavioural budgets (Mann et al., 2000) and will affect the content and rate of their vocal behaviour. Future studies of wild bottlenose dolphins and harbour porpoises should attempt to assess the vocal behaviour recorded by C-PODs for other visually observable behaviours such as mating and socialising.

Communication trains have been described from harbour porpoises with ICIs shorter than those in feeding buzzes (Clausen et al., 2010). The extent of the use of such trains is not known, but the data show that, regardless of their actual function, more clicks with short ICIs are produced during foraging than during travelling for harbour porpoises. It is not possible to distinguish unsuccessful feeding attempts (approaches to a target) from those that end in prey capture and, therefore, an increase in feeding buzzes does not necessarily indicate an increase in feeding. However, it should at the very least indicate areas where foraging takes place, which in itself is critical information for conservation and management purposes.

Regardless of the fact that the C-POD does not record the full vocal repertoire produced by these animals, nor does it select all the recorded clicks for its final click train classification, it can reveal valuable behavioural information about its target species by detecting potential foraging events, making C-PODs particularly useful for long-term monitoring studies. These devices can be used to identify important feeding areas, particularly for harbour porpoises but also potentially for bottlenose dolphins. Nevertheless, further studies to extract click trains that bottlenose dolphins use during foraging from C-POD data are recommended. Behavioural observations using visual methods are limited to calm seas and daylight hours, typically during summer months. Therefore, acoustic monitoring is the only way to acquire detailed information on foraging patterns for animals that are known to forage nocturnally. The C-POD detects and identifies cetacean vocalisations based on a complicated algorithm, and its detection capability is dependent on the acoustic properties of the target sound, the surrounding ambient noise, and the animal behaviour, as well as the actual sensitivity of the device. In recent years, many such devices and algorithms have been developed and will hopefully continue to be developed and improved to the benefit of researchers, decisionmakers, and the conservation of coastal cetacean populations. The C-POD, like other similar acoustic devices, is designed for long-term static acoustic monitoring (SAM) and enables researchers to monitor cetacean presence in larger spatial and temporal scales than previously may have been possible. It, as with any other method, does have its disadvantages, and due to the nature of its click train detection, some individual clicks will always go undetected. It is therefore imperative to recognize that although SAM devices may be very useful in detecting long-term trends of presence, or in fact in identifying feeding areas, they should not be used for analysing vocal behaviour in great detail. An important advantage of the static acoustic click logger over traditional acoustic methods is the reduced amount of data incurred and the automated species recognition process, both of which speed up the data analysis. In addition, describing behaviour through acoustic methods removes biases associated with visual descriptions of behaviour, ultimately facilitating comparisons of data between studies and across regions.

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